

**Glossobalanus marginatus, a new
species of Enteropneusta from the North Sea.**

By

Alexander Meek.

With 14 Text-figures.

THE only species of Enteropneusta which have been recorded from the area of the British Isles are two species of the genus *Dolichoglossus*, one from the west coast of Ireland (Ballynakill Harbour—Tattersall, 1905), the other from the west coast of Scotland (Sound of Mull—Assheton, 1908). These presumably, like other species of the genus, have an embryonic development. The occasional capture of *Tornaria* off the coast of Ireland, in the Irish Sea, in the Channel, and at St. Andrews have indicated that *Balanoglossus* and its allies occur also in the area, but hitherto such have evaded capture. The specimen about to be described was captured off the Farne Islands and thus extends the range of the group to the east coast and the North Sea, and it has the further importance of belonging to a genus and a family the members of which more than probably pass through a larval phase. The specimen was obtained during a survey made off the coast of Northumberland by the Ministry of Agriculture and Fisheries at a depth of about 52 fathoms off the Longstone, the instrument in use being a small Petersen grab. The position of the boat at the time (9 a.m. on August 22, 1921) was $55^{\circ} 33' N.$, $1^{\circ} 7\frac{1}{2}' W.$ I have to thank the scientific staff for kindly submitting the specimen to me for description.

1. THE ADULT.

External Characters.—The specimen is the anterior end of a mature male and measured longitudinally, proboscis

7 mm., collar 5 mm., and the trunk, which was cut off at the end of the genital region, about 50 mm. At the posterior end the beginning of the region of the liver caeca was fortunately included. The specimen, as Text-fig. 1 shows, was bent at right angles in the post-branchial region.

The colour after preservation in spirits is brown, due as will be seen to dark pigment-cells lodged internally to the

TEXT-FIGS. 1, 2, AND 3.

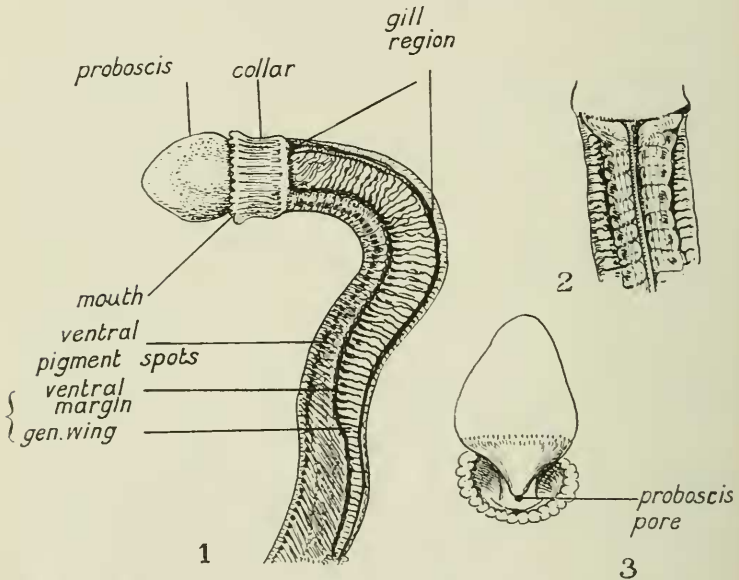


Fig. 1.—View from left side of anterior end.

Fig. 2.—Ventral view of the anterior end of the trunk to display folds of oesophageal region which is limited on either side by the ventral genital groove.

Fig. 3.—Dorsal view of proboscis showing proboscis pore.

longitudinal muscles of the body-wall. The proboscis is almost white and the gonads yellow. The brown colour marks the collar, on the trunk it differentiates the ventral body-wall from the genital wings. The yellow-coloured gonads stand out prominently on the wings, and the brown colour which intervenes between them and the body-wall

helps to define them. Ventrally on the trunk the brown pigment is concentrated to form a paired series of dark spots which lie one on each side of the ventral median line.

The proboscis is short and rounded, laterally compressed in front and expanded on each side near the collar. At this point it measures transversely 5 mm. It narrows again rapidly to form a neck of attachment to the collar, which provides a recess for its reception. The neck dorsally presents a single median proboscis pore. Behind the pore an opening on the anterior wall of the collar may be artificial, but it is in the position of the neuropore (Text-fig. 3). The proboscis was cut in two transversely before the specimen reached me. The interior is a wide cavity which, as has been said, communicates with the exterior by a median proboscis pore. Basally it presents a simple diverticulum or so-called notochord, and there is no vermiform process.

The collar is markedly muscular. It forms a folded edge anteriorly, and it is occupied around the middle of its length by a groove. It is rounded in section and the groove measures about 5 mm. in all diameters. The collar is also defined posteriorly by an edge, but passes after a slight depression into the trunk.

The trunk is resolved externally into the ventral body-wall and the genital wings, and these are separated by a lateral groove which, like the genital wing at first gradually and posteriorly more rapidly, is carried towards the dorsal aspect of the body (Text-fig. 1). The wings are occupied by the gonads in the form of irregularly folded but on the whole transverse ridges which project from the surface. They are large and in the specimen approximated over the dorsal region of the body so as to occlude the latter from the exterior.

The genital wing of the left side is larger transversely than that of the right, and this mark of asymmetry is emphasized by the sinuous path of longitudinal features of structure like the dorsal groove between the genital wings, the ventral nerve-cord, and the paired series of pigment spots. The

ventral line is carried to the left, then to the right, and again to the left. At the posterior end of the body, which is laterally flattened, the ventral angle is not that of the ventral nerve but to the right of that line (Text-fig. 4).

A still more noteworthy feature of the exterior is the presence of folds of the body-wall, the glandular folds of Spengel. In front they are irregular but mainly transverse (Text-fig. 2); behind the gill region they become markedly

TEXT-FIGS. 4 AND 5.

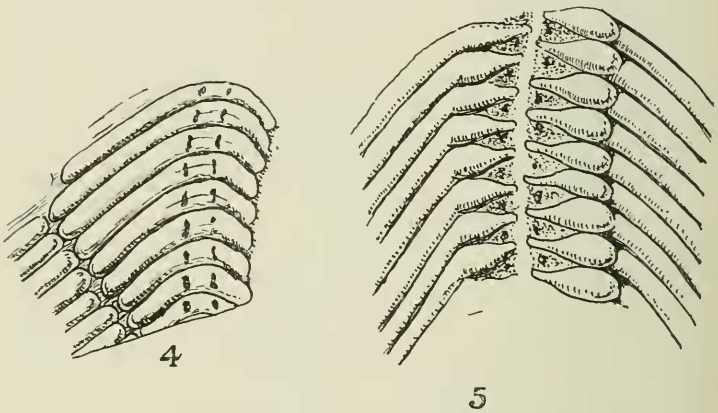


Fig. 4.—Internal surface of alimentary canal at the posterior cut end of the specimen—the region of the liver caeca—to show the disposition of the folds and the real median line to one side of the actual median line. The upper end is anterior.

Fig. 5.—External view of the body-wall at the posterior end of the genital region to show the condition of the folds on either side of the ventral nerve-cord.

transverse on that part of the body-wall below the genital wings, the area occupied increasing as that of the genital wings diminishes. In this posterior portion of the specimen (Text-fig. 5) they emerge from the mid-ventral line as narrow folds which expand into a club shape and narrow again, either ending abruptly or passing into oblique folds of the body-wall. If they end they do so in a series which defines a longitudinal groove, and similar but usually oblique grooves

are formed by the folds ending in succession along the same line. Posteriorly the lateral walls are occupied by grooves and folds which pass in this manner from the ventral aspect upwards and backwards. The condition ventrally of the folds is remarkably similar to that described by Spengel in the case of *Glossobalanus elongatus* from the Gulf of Naples. The only difference is that in the North Sea specimen the folds are fairly regular in size, whereas in the Naples form they were alternately large and small. Spengel pointed out with regard to them: 'Mir ist eine solche Anordnung, die sicher bei *Gl. sarnienseis* nicht vorkommt, bis jetzt von keiner Enteropneustenform bekannt.' It may be remarked that the Naples specimen is asymmetrical much as the North Sea one is asymmetrical.

The right series of gonads end slightly in front of the left and give place to the liver caeca in the form of diverticula of the gut and the body-wall on either side of the mid-dorsal groove which emerges from between the genital wings. At this posterior end of the specimen it is seen that the external folds are paralleled by folds of the wall of the alimentary canal (Text-fig. 4).

It is impossible from the strongly approximated condition of the genital wings to state the length of the branchial region, and it will be as well here to anticipate the further description and to complete our review of the external characters by saying that it is about 15 mm. This region is covered externally by the large genital wings so that the usual triangular space behind the collar is reduced to a slit and even basally next the collar the space is not very wide (Text-fig. 1). It is further to be observed, not merely by the presence of a groove which delimits the genital wings from the ventral body-wall of this front region of the trunk, that the branchial region is defined from a widely expanded oesophageal region.

These features, the distinct oesophageal chamber below the branchial region, the absence of a vermiform process to the diverticulum, the presence of liver caeca, the single median

proboscis pore, all lead to the impression that the specimen belongs to the family Ptychoderidae. This family includes the genera Ptychodera, Balanoglossus, and Glossobalanus, and it has already been seen that the specimen bears some undoubted claims to affinity with Glossobalanus.

Now there is no better region of the body which may be appealed to for the purpose of settling which genus is the right one than the post-branchial region. In Ptychodera the gills open by wide lateral slits, in the others by small pores. In Ptychodera the gonads open by many openings on the inner aspect of the genital wings, in Balanoglossus by a single series of pores near to the gill-pores, in Glossobalanus by a single series of pores on or near the margin of the genital wings.

I felt justified, therefore, in excising and cutting into sections a small part of this region. Unfortunately the specimen was indifferently preserved, and had to be subjected to several changes of alcohol. Good sections were therefore not to be expected and they were not obtained. The internal epithelium suffered most, as Spengel found in the case of *Glossobalanus elongatus*. But the general morphological features were quite well displayed, and in the case of the gonads in particular even histological detail.

Before proceeding to describe the more important features displayed by the sections it is obvious that the presence of synapticula shows that we were right with regard to family, and the opening of the gonads near the margin and the disposition of the lateral septum indicate that the genus to which the specimen belongs is *Glossobalanus*. The specimen agrees also with the majority of the species in possessing a comparatively short branchial region.

Post-branchial Region.—A portion of about 6 mm. of this region was removed and cut into transverse sections and Text-figs. 7-11 are from slides 1, 11, 19, 22, 23, and 24. Text-fig. 12 is taken from slide 16, and Text-fig. 13 from slide 4. The sections show that in spite of the large genital wings the specimen is structurally a *Glossobalanus*. The asym-

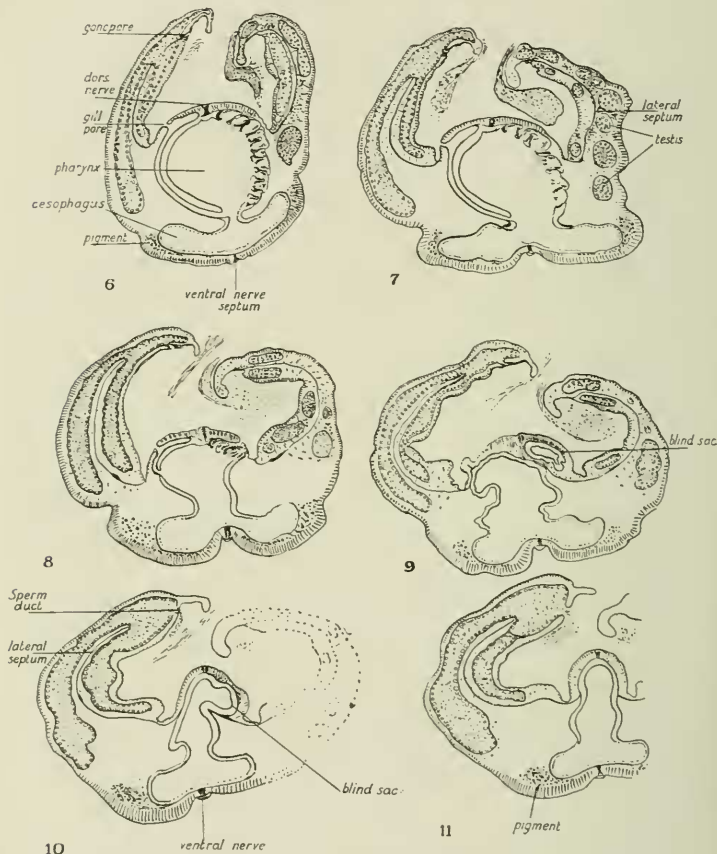
metry is apparent, and, as has been seen, it is not produced altogether by distortion.

The body is enclosed in a dorsal and ventral wall and on each side is expanded into the genital wings, and the body-wall at the origin of the wing on each side presents distinct grooves—dorsal and ventral genital grooves. The ventral groove has already been observed externally and extends, as has been noted, from the collar to the end of the genital region. The dorsal genital groove likewise extends along not merely the branchial region but the whole of the genital region. The alimentary canal is resolved into a large dorsal pharynx and a wide oesophagus. The walls of the pharynx are perforated by gills opening into gill-pockets which are provided with openings in succession along a line medially situated to the dorsal genital groove on the dorsal wall of the body. The gills have the typical enteropneustan structure. The gill septa or primary bars present ridges externally and are supported by skeletal plates, which are conjoined and forked internally and ventrally. Intervening between them are the tongues or secondary bars, which are likewise supported by a pair of plates, but these are not fused. They lie on either side of a narrow diverticulum of the body-cavity, thus not very far apart. They end below at the free end of the tongue. They are connected at intervals with the primary bars by synapticula and the slits are thereby converted into a fenestrated succession of openings in each case (Text-fig. 13). I have not been able to find out exactly the number of synapticula, but successive sections indicate the number to be about ten. Nor can I state definitely the number of gills, but measurements made from the sections and from the specimen show that the number is about forty to forty-five on each side.

The medial line is marked above and below by the dorsal and ventral mesenteries with the dorsal and ventral nerves and vessels. The circular layer of muscles is very thin. The longitudinal muscles reach their highest development on the ventral wall of the body. They are still well developed

along the outer wall of the genital wing, but they are small on the inner wall of the wing and rise again distinctly on the

TEXT-FIGS. 6-11.



Figs. 6-11.—Transverse sections of the post-branchial region. The left side is on the reader's left. The reconstructed relationship of the gonad and gill is shown on the left side, the section as cut on the right.

medial side of the gill-pores. As usual the space immediately at the side of the dorsal and ventral mesenteries is devoid of muscle, and along the line of the gonopores there

is certainly an interruption, along the line, that is to say, which Spengel defines as the sub-median line.

The genital wings are large and bend over the dorsal part of the body to arch over a spacious atrial cavity. The gonads occupy the wings and are resolved each into outer and inner lobes, both much folded, but they amalgamate near the summit of the wing to open by a pore not at the margin but near it on the inner face of the wing. The margin of the wing beyond the series of gonopores is a thin flap which is reflected or may be reflected over the openings and serves to occlude that part of the atrial cavity. The outer lobe of the gonad is continued into this margin so that a short third branch is present. In this respect the specimen indicates an approach to the condition of *Balanoglossus*, and is distinct from all the described species of *Glossobalanus*. An indication of the displacement of the gonopore on the inner side of the genital wing is shown in Spengel's drawing of *Glossobalanus minutus*.

In the anterior end of the branchial region it is evident that the gill-pores and the gonopores come into closer relationship, but with the expansion of the genital wings they are carried apart reaching the condition figured. An inspection of the specimen shows, moreover, that posteriorly, that is to say behind the branchial region, the gonopores still occupy a high position on the wings. Several authors have attempted to show that a relationship exists segmentally between the gonopores and the gill-pores, and in this specimen this appears to be the fact, for the succession of the gill-pores is accompanied by a succession of gonopores. In other words the region cut into sections bears the same number of each. There are about five gonopores to 2 mm. in the post-branchial region, and if the same distance between them is retained over the length of the genital region there ought to be some 120 pairs of gonads and gonopores.

The outer and inner lobes of the gonad are separated by a lateral septum which extends from the region of the line of the gonopores to the dorsal genital groove, and it is

displayed in all the sections figured. This is the disposition of the septum in the branchial region, but with the disappearance of the gills the septum is extended medially to be attached to the upper part of the post-branchial alimentary canal. It is obvious, therefore, that in the branchial region of the body the septum forms a cavity for the inner branch of the gonad, and that this cavity excludes this branch of the gonad from the space between the dorsal wall of the body and the branchial region of the alimentary canal; or, to put it another way, from the space between the dorsal

TEXT-FIGS. 12 AND 13.

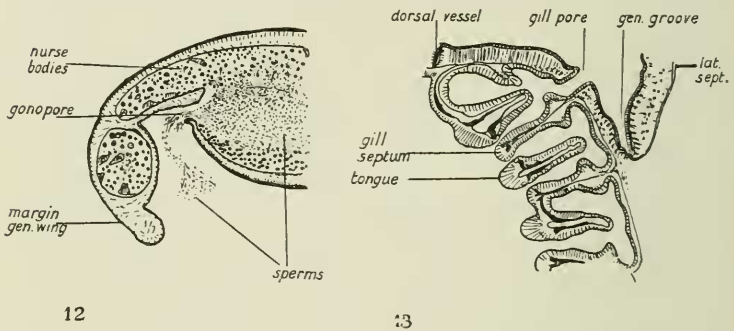


Fig. 12.—A more detailed view of a section of the margin of the genital wing through the gonopore.

Fig. 13.—Section through a gill-pore of the right side to show disposition, the gill skeleton in section with synapticula, and the insertion of the lateral septum to the genital groove.

genital groove and the dorsal mesentery. The gill-pores are, therefore, not merely medial to the gonopores, they are medial to the gonad. The outer lobe could certainly penetrate this region but it does not do so. It is only behind the branchial region that the displacement of the septum to the wall of the gut permits of the inner branch of the gonad invading this region of the body cavity. This is a feature of importance, for it is the disposition of the septum and the gonad in the genus *Glossobalanus*, and it has been discussed by Spengel in the monograph and in his paper on *Glosso-*

balanus elongatus (1904). The septum is a double one and transmits the lateral vessels to the wing. It is also connected by strands to both the inner and outer walls of the wings and here also the pigment cells occur. The pigment cells are found also under the muscles of the dorsal wall of the body, between the oesophageal region of the alimentary canal and the muscles of the ventral body-wall, and on either side the pigment expands into conspicuous masses which rise and fall with the folds of the body-wall, as has been noted.

In the above respects the specimen is very like other species of *Glossobalanus*. There is a close resemblance also with reference to another feature, with at the same time a distinction of importance and morphological interest (Text-figs. 8-11). At the posterior end of the branchial region the gills become short and relegated to the dorsal side of the region. The shortening of the gills is accompanied by a gain of the narrow part of the alimentary canal intervening between the pharynx and the oesophagus. As soon as the gills end this upper part of the tube suddenly expands dorsally and projects as a short diverticulum over the posterior gills of the right side, and in this region the dorsal mesentery is lengthened on the inner side of the diverticulum. The other species of *Glossobalanus*, as Spengel has shown, present such a diverticulum, but in all evidently it is a median one, or nearly so, in front of which a similar lengthening of the dorsal mesentery has been remarked. The condition of the North Sea specimen is therefore like that of the others, but it differs in the outgrowth being asymmetrical. It is scarcely necessary to say that the blind sac recalls in its position and its origin the hepatic diverticulum of *Amphioxus*.

The North Sea specimen is a male in the act of spawning. Most of the gonads in the region of the sections are empty or nearly so, and the sperms are collected in two masses which occupy the sides of the atrial cavity. The lateral masses are due not only to their issuing from the gonads of each side but to the branchial current which tends to separate

them. But they are enclosed in a mucous-like secretion probably derived from the ectodermal gland-cells of the atrial cavity. The secretion, however, is present in the neighbourhood of the pore and plays its part in directing the sperms laterally. The mass is tucked in within the space formed by the margin of the genital wing and spreads outwards as a thin sheet outside the marginal flap. The anterior gonads appear to discharge their contents before the posterior and the left before the right. In the sections the sperms may be easily seen issuing from the gonopores and joining the mass below, a mass containing countless numbers, each having the usually flagellate shape with a rounded head.

Besides the sperms the gonadial sacs are occupied by bodies which are highly refringent and eosinophile, and in the latter respect in striking contrast to the sperms. Like the sperms they arise in marginal cells and become detached. They vary greatly in size and appear to have a protoplasmic envelope, and the bodies, though usually apparently homogeneous, have sometimes an appearance as if they were made up of a mass of smaller bodies. They are not as far as can be seen nucleated. In the undischarged or partially discharged folds of the gonad they surround the mass of sperms which occupies the centre, but small groups of sperms are found amongst them peripherally. In the discharged parts of the gonads they press into the interior, but whether this is due to collapse of the tube or to actual multiplication could not be said. A few escape with the sperms and are seen in the atrial mass and there appear to lose gradually their eosinophile character. In the gonads also here and there are large cells of the margin which project into the cavity each provided with a large nucleus containing a large nucleolus. The refringent bodies have been observed in other specimens of *Enteropneusta*, and so far as can be said at present they may be regarded as nurse-bodies.

It is possible that the peculiar condition of the atrial cavity is due to the fact of the discharge of the sperms. In the male the apposition of the genital wings may be

necessary at that period to prevent the escape of the sperms while the creature occupies the burrow. But even so it must be acknowledged that the marginal outgrowth is a morphological feature, and this has been indicated in the specific name chosen for the species, which is further characterized by (1) the brown pigment cells and their concentration into a double series of ventral pigment spots; (2) the asymmetrical condition of the body, the blind sac, and the genital wings; (3) the large size of the genital wings; (4) the short third branch of the gonad. The depth at which the specimen was obtained, 52 fathoms or 95 metres, may also be a peculiarity.

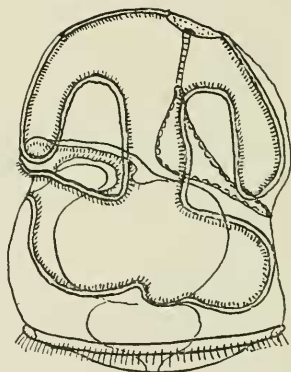
2. THE LARVA.

The adult is not common and probably occurs in isolated communities, one of which lies off the coast of Northumberland. An enteropneustan larva has been got rarely in the North Sea, and it is worth while inquiring whether it is likely related to *Glossobalanus*.

On August 6, 1890, a *Tornaria* was captured at the surface in St. Andrews Bay, and I made a drawing of it in the living condition in the Marine Laboratory there. This drawing I reproduce (Text-fig. 14). It will be seen to be very like a figure published by Bourne (1890) of a *Tornaria* captured over deep water in the Channel. His figure 13 and the one I now give are so similar as to lead to the opinion that they belong not merely to the same genus but to the same species. The anterior region is broad, the apical plate somewhat dorsal to the mid-longitudinal line and occupied by a pair of optic pits, the pre-oral and post-oral ciliated bands are simple not presenting lateral folds or processes, there is a slight characteristic bending of the transverse part of the post-oral band, the stomach and intestine are wide. A *Tornaria* of this type, and agreeing completely with the St. Andrews example, was captured on July 27, 1921, off the Longstone, during a plankton trip of the *Eradne*, in the mid-water net. Bourne regarded his specimen as a fully-developed larva. A similar

larva is got at Heligoland, and at St. Andrews Professor McIntosh says it is obtained fairly regularly in August and September. In the Channel another kind of larva is also procured, *Tornaria krohnii*. *Tornaria krohnii* is distinguished by a more conical shape anteriorly, by the longitudinal ciliated bands being thrown into folds, and by the stomach and intestine being narrow comparatively. This larva is common in the Mediterranean, and it is common inshore at Plymouth. Dr. Lebour was good enough to send

TEXT-FIG. 14.



Tornaria captured at St. Andrews, August 6, 1890, which it is suggested may be the larva of *Glossobalanus*.

me examples from the Plymouth plankton and they all are *Tornaria krohnii*, and Bourne had already stated that the inshore larvae were *Tornaria krohnii*. Since Heider (1909) obtained so fortunately early stages of *Balanoglossus clavigerus* which he found to agree with early stages of *Tornaria krohnii*, Stiasny (1913) has been able to follow the history in greater detail, and there appears to be little doubt that *Tornaria krohnii* is the larva of *Balanoglossus clavigerus*. This species is common on the south side of the Channel and on the north-west coast of France.

At the west end of the Channel it appears then that there

are two types of larvae, one of which is more than likely the larva of *Balanoglossus clavigerus*, and the other somewhat but not widely different. There are also found on the south side of the same region two nearly related genera, *Balanoglossus* and *Glossobalanus*, the latter with the species *G. minutus* and *G. sarnienseis*. It is possible that the second type of larva is connected with *Glossobalanus*, and if the evidence be extremely slender it gains a little in weight by the fact that the same type of larva and adult are present in the North Sea. Bourne's larva may thus be related to either *G. minutus* or to *G. sarnienseis*, or it may refer to a species which is not obtained inshore but at some depth and not yet discovered.

The North Sea type of larva is not unlike that described by Agassiz and by Morgan from the Atlantic coast of the North Atlantic, and a similar larva also occurs on the coast of California (Ritter and Davis, 1904).

SUMMARY.

The specimen described was captured off the Northumberland coast on August 22, 1921, and its discovery extends the range of the Enteropneusta to the North Sea and to the east coast of the British Isles. It also adds a new genus to the British list. It belongs to the family Ptychoderidae and to the genus *Glossobalanus*, but it presents features which indicate that it is a new species which has been called *Glossobalanus marginatus*. It has been suggested that it may be related to a larva which has also been found in the North Sea.

It is a pleasure to express grateful thanks to Sir S. F. Harmer and Mr. Kirkpatrick of the British Museum of Natural History—to the former for valuable guidance in literature, and to the latter for an opportunity of examining the museum's collections of Enteropneusta.

LITERATURE.

1. ADULT.

- Assheton (1908).—'Zool. Anz.', Bd. 33.
 Caullery et Mesnil (1904).—'Zool. Jahrb. (Anat.)', Bd. 20.
 Spengel (1893).—'Fauna u. Flora d. Golfes v. Neapel', Monogr. 18.
 — (1902).—'Zool. Jahrb. (Syst.)', Bd. 15.
 — (1904).—'Zool. Jahrb. (Anat.)', Bd. 20.
 Tattersall (1905).—'Dept. Agr. and Tech. Inst. for Ireland. Sc. Invest.',
 1902-3.

2. LARVA.

- Agassiz (1873).—'Mem. Amer. Acad. of Arts and Sci.', vol. 9.
 Bateson (1884-5).—'Quart. Journ. Micr. Sci.', vols. 24-5.
 Bourne (1890).—'Journ. Mar. Biol. Ass.', vol. 1.
 Heider (1909).—'Zool. Anz.', Bd. 34.
 Morgan (1891, 1894).—'Journ. of Morph.', vols. 5 and 9.
 Ritter and Davis (1904).—'Univ. of California Publ. in Zool.', vol. 1.
 Stiasny (1913).—'Zool. Anz.', Bd. 42.
 — (1914).—'Zeits. wiss. Zool.', Bd. 110.